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When prey provide more than food: mammalian predators appropriating the refugia of their prey

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Abstract Some mammalian predators acquire both food and shelter from their prey, by eating them and using the refugia the prey construct. I searched the literature for examples of predators that exhibit this behavior and summarize their taxonomic affiliations, relative sizes, and distributions. I hypothesized that size ratios of species involved in this dynamic would be near 1.0, and that most of these interactions would occur at intermediate and high latitudes. Seventeen species of Carnivorans exploited at least 23 species of herbivores as food and for their refugia. Most of them (76.4 %) were in the Mustelidae; several small species of canids and a few herpestids were exceptions. Surprisingly, the average predator/prey weight ratio was 10.51, but few species of predators were more than ten times the weight of the prey whose refugia they exploit. This may be why the long and thin Mustelines commonly exploit this habit. A number of predators appropriate the refugia of their key prey during winter when their prey occupies thermally secure nests. Indeed, most of the predator–prey pairs that engage in this relationship occur in intermediate and high latitudes, though there may be a reporting bias. Predators that depend on prey as food and for shelter, and whose fates are linked strongly to a few key prey species, may be particularly vulnerable to changes in climate that affect the subnivean habitats of their prey. Mammals that create refugia that can be used by other species (among them predators) may play disproportionately important roles in their communities.

Keywords Predator–prey · Dens · Herbivore · Behavior · Habitat · Resting · Foraging

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Introduction

Mammals require food and most require shelter, either to protect them from predators or from thermal stress. Carnivorous mammals are unique in that they subsist on mobile food sources which, particularly if these sources are vertebrates, may build their own refuges to help regulate their body temperatures or to hide. Predators have the following options for the source of their shelter; they can either (1) create their own refuge, (2) use a vegetation or a geologic feature (e.g., tree hollow, rock crevice), or (3) use or appropriate the refuge originally created by another species. Many mammalian carnivores use the first option and have the capability of digging their own burrows or dens in soil or snow (e.g., European badger, *Meles meles* [Dunwell and Killingley 1969]; American badger, *Taxidea taxus* [Lindzey 2003]; wolverine, *Gulo gulo* [Copeland and Whitman 2003]). Others use natural cavities in trees or rocks (e.g., common genet, *Genetta genetta* [Lariviére and Calzada 2001]; ringtail, *Bassariscus astutus* [Gehrt 2003]; gray fox, *Urocyon cinereoargenteus* [Cypher 2003]). This review, however, is focused on understanding the frequency and circumstances that occur in the third case, when mammalian predators appropriate the refuges of prey for their own use, sometimes after having killed the occupant.

Accounts of predators using the refugia of other species remain few, largely unquantified, and based primarily on casual sightings and reports (Murdoch et al. 2013). I sought to highlight the prevalence of this behavior, since it has not been

formally brought to the attention of the scientific community. In this paper, I review the species of carnivores that appear to have evolved a habit of preying on species that also provide them shelter when they co-opt their refuges (e.g., nests, burrows, dreys, dens). I review the taxonomic distribution of the occurrence of this behavior and I hypothesize that size ratios of species involved in this dynamic would be near 1.0. This is expected for two reasons. First, to be able to physically occupy the refuge of a prey species, the predator must not be that much larger than the prey. Second, to be able to subdue and kill the prey species, the predator must not be that much smaller than the prey. I also expected most of these interactions would occur at intermediate and high latitudes because these regions are colder in winter and a predator that usurps the refuge of their prey will also reap the thermal benefits.

In cases where a predator kills and appropriates the refuge of its prey, the prey species represents an important *habitat* resource for the predator. This is distinct from the situation that occurs when predators search the refugia of prey but do not appropriate the prey's resting sites for their own or when a predator occupies the refuge of an herbivore that is not included in its diet. I exclude these circumstances from consideration. For example, the Pallas's cat (*Otocolobus manul*) and corsac fox (*Vulpes corsac*) use the burrow system of the Siberian marmot (*Marmota sibirica*) for resting, but do not prey on this species (Murdoch et al. 2010; Ross et al. 2010a, b). Similarly, non-trophic relationships occur between the red fox (*Vulpes vulpes*) and woodchucks (*Marmota monax*) and between meerkats (*Suricata suricatta*) and Cape ground squirrels (*Xerus inauris*) (Stanley 1963; van Staaden 1994). Carnivores can also use termitaries as refuges without eating termites (e.g., common dwarf mongoose, *Helogale parvula* [Rasa 1983]; striped weasel, *Poecilogale albinucha* [Lariviére 2001]). The converse is also true: a termite-eating Carnivoran, the aardwolf (*Proteles cristatus*), enlarges the burrow of the springhare (*Pedetes capensis*) to use as its den, but does not prey upon it (Anderson and Richardson 2005). A number of other species of carnivores use abandoned dens (usually burrows in soil) of species that they do not hunt, presumably to avoid the energetic cost of creating their own. Finally, I consider in this review primarily prey and predators species that have evolved together; exotic or invasive species are not generally considered.

I predict that only species of predator that are relatively small, compared to their prey, may be able to exploit the use of their prey's refugia. Thus, I also report the weights of predators and prey, and their ratios. And, because this phenomenon may be more important to species of predators that require refugia in cold climates, I also report the latitudinal distribution of pairs of species that have been described as engaging in this dynamic. Because the literature is uneven on the depth of published ecology and behavior for mammals, I assume that there are more mammals that exhibit this unique foraging and resting pattern than reported here. Thus, I describe the taxonomic affiliation, geographic location, and relative body sizes of species that exhibit such a relationship with the goal of identifying characteristics that may make it easier to predict whether other species, that are more poorly studied, may also be among them. I summarize the species of mammalian carnivores that appropriate the refuges of their frequent prey and discuss the variation in the behavior across taxa and some implications for the conservation of these species under changing environmental conditions.

Materials and methods

I reviewed the literature via internet searches (Google Scholar™, Web of Science™) using the search terms "predator prey," "foraging," "dens," "rest sites," and "refugia," entered separately or in combination with common and/or scientific names of individual taxa. I also searched my own extensive library of literature on carnivore ecology and consulted with colleagues to discover information on species of carnivores that appropriate the refugia of their prey. I reviewed information about the diet of predators and resting habitats of predators and prey because knowledge of each was necessary to understand how these ecological characteristics are related. My goal was to reveal from the published literature as many instances of appropriation of prey refugia as possible. Not all species have been studied sufficiently to know their habits in this respect and not all the literature may have been available for electronic searches. Thus, my discoveries are but a sample of them, revealed using all the means at my disposal.

The nature of the evidence necessary to determine if a species of predator kills and then appropriates its refuge is usually circumstantial. For example, even though predator x is found using a refuge created by its prey y, it rarely can be determined that x killed the particular individual of species y that created the specific refuge that is being occupied by the predator. The predator may have searched the refuge and found it unoccupied and simply used it from that point forward. However, I assumed that when a predator occupies the refuge created by a prey species frequently enough to be reported in the literature, and when that prey species has been demonstrated to be an important food item in the predator's diet, that the predator has developed a unique foraging strategy that exploits the combined benefits of food and shelter provided by a prey species. These species and their prey are reported here. All body weights were taken from a published database of

weights of late quaternary mammals, averaged between sexes (Smith et al. 2003).

Results

I discovered evidence of 17 species of mammalian carnivores exploiting at least 23 species of prey as food and appropriating their refugia for the carnivore's use (Table 1). Thirteen of the 17 species (76.4 %) were in the Mustelidae (weasels and relatives), the majority (n=8) of which were in the subfamily Mustelinae. The balance of the species were in the Herpestidae (two species of mongoose) and Canidae (two species of fox) (Table 1). The prey ranged in size from termites (Blattodea)—whose mounds are used by a mongoose that also feeds on termites (the yellow mongoose, *Cynictus pencillata*)—to the approximately 8 kg Siberian marmot (*M. sibirica*) whose burrows are appropriated by the steppe polecat (*Mustela eversmanni*) (Table 1). Of the 17 species of predators, the steppe polecat exploited the refuges of the greatest number of prey (sousliks, marmots, hamsters, jerboas, and zokors) (Table 1). The refuges co-opted by the predators were most often burrows in soil (n=18) or nests made of vegetation (grass, leaves, or sticks; n=10) (Table 1).

The ratios of weights of predator/prey of averaged (SD) 10.51 (18.55), excluding the mongoose/termite pair. Most of the ratios were less than 10.0 (Fig. 1). The four outliers, with values >20.0 (ranging from 24.7 to 57.7) were the steppe polecat—striped desert hamster, the steppe polecat—jerboa, the kit fox—kangaroo rat, and the swift fox—kangaroo rat.

Discussion

The species most frequently reported killing and appropriating the refuges of their prey were in the subfamily Mustelinae (weasels, mink, ferrets, and polecats). This is not surprising given their small size and the fact that they are adapted to hunt within the burrows of their mammalian prey (King and Powell 2007). The most abundant literature on the behavior references *Mustela erminea*, *Mustela frenata*, and *Mustela nivalis* which kill voles or lemmings in the winter and occupy their enclosed nests (MacLean et al. 1974; Fitzgerald 1977; Feige et al. 2012). Other weasels may also exhibit this behavior, but little is known of their ecology and behavior in this respect. For example, the African striped weasel preys primarily on small mammals in grassland communities and pursues rodent prey in their burrows (Lariviére 2001)—characteristics that suggest that they too may kill and occupy prey refugia. Indeed, in captivity, striped weasels carry their prey back to their nest box (Rowe-Rowe 1978) suggesting that if their natural prey creates nest structures as refuges, the African weasel may likely co-opt them for their own use.

The second most common taxon reported appropriating the refugia of their prey are species within the subfamily Martinae (e.g., martens, sables). Appropriating prey refuges appears to be less common in this group than it is for the weasels, but it includes co-opting the winter cone caches/dens or the dreys of tree squirrels and the burrows of mountain beavers (Table 1). However, although remains of the squirrels are reported in the diet, it is possible that in some cases, the predator and prey species coexist at rest sites, as Buskirk (1984) suggested. The frequency with which species in the family Mustelidae co-opt the refugia of their prey highlights the importance of the relative sizes of predators and prey to its prevalence. Of the sample of species pairs reported here, most of the carnivores are no more than ten times the weight of their prey. Larger predators have, of course, an advantage in subduing smaller prey, but their larger size makes it less likely that they can occupy the prey's refuge. Perhaps, this is why the long and thin Mustelines have been reported to exploit this habit most often. Their body masses are equivalent or just larger than most of their prey but their thin and flexible body shapes allow them to exploit the refuges of common prey. Future studies on this subject should focus attention on predator–prey combinations with body weight ratios <10, especially among the Mustelidae.

The frequency of this behavior in the Mustelinae and Martinae may be due, in part, to a Holarctic bias in research and reporting and paucity of autecological studies on small carnivores in the tropics. Species in these subfamilies primarily occur in northern latitudes and this is where many of the researchers live and work. Of the species pairs where the phenomenon of appropriating prey refugia has been reported, the great majority (90 %; n=27) occurred at intermediate latitudes (20–40° north or south). Only one example of the phenomenon, the Egyptian mongoose—European rabbit pair, occurred at latitude <20°. It is possible that this is because there are so many fewer studies on small and intermediate-sized carnivores and their prey in the tropics. A Google Scholar search revealed results that often exceeded 5000 references for many of the species in pairs that occur at temperate zones (intermediate latitudes) (Table 1). Compare this, for example, to the number of studies on tropical species such as the Liberian mongoose (*Liberiictis kuhni*; 67 results) or the Nilgiri marten (*Martes gwatkinsii*; 74 results). Thus, it is possible that the frequency of this predator—prey phenomenon, and its latitudinal distribution, is influenced by where the species occur and, as a result, the depth of ecological and behavioral knowledge about it. Alternatively, carnivores in equatorial regions may also be underrepresented here because they do not typically experience the temperature extremes that require their prey to create refugia to buffer them from thermal stress during cold winters or cold nights. For example, the reason that weasels and martens are so often reported killing prey whose refugia they then appropriate is because they do so primarily

Table 1 Reported observations of species of mammalian predators that use a refuge created by one of their prey species

Predator species	Predator weight (g)	Prey species	Prey weight (g)	Predator/ prey weight	Type of refuge	Latitude[a]	Number of Google Scholar references Predator/prey	References
Ermine (*Mustela erminea*)	168.8	Montane vole (*Microtus montanus*)	36.3	4.65	Herbaceous nest (winter)	Intermediate	9250/5830	Fitzgerald (1977)
Least weasel (*Mustela nivalis*)	77.3	Collared lemming (*Dicrostonyx groenlandicus*)	54.4	1.42	Herbaceous nest (winter)	High	8300/1870	MacLean et al. (1974)
		Siberian lemming (*Lemmus sibiricus*)	52.3	1.48	Herbaceous nest (winter)	High	8300/1170	Feige et al. (2012)
Long-tailed weasel (*Mustela frenata*)	147.0	Montane vole (*Microtus montanus*)	36.3	4.05	Herbaceous nest (winter)	Intermediate	11,900/5830	Fitzgerald (1977)
American mink (*Neovison vison*)	945.0	Muskrat (*Ondatra zibethica*)	981.5	0.96	Lodge and/or soil burrow	Intermediate	16,000/6160	Errington (1961, 1963)
Black-footed ferret (*Mustela nigripes*)	850.0	White-tailed prairie dog (*Cynomys leucurus*)	908.5	0.94	Soil burrow	Intermediate	3250/2260	Sheets et al. (1971); Campell et al. (1987); Clark (1989)
		Black-tailed prairie dog (*Cynomys ludovicianus*)	1364	0.62	Soil burrow	Intermediate	3250/5700	
Steppe polecat (*Mustela eversmanni*)	1350	Souslik (*Spermophilus citellus*)	290	4.65	Soil burrow	Intermediate	1230/3440	Zverev (1931); Brom (1954); Stroganov (1969)
		Siberian marmot (*Marmota sibirica*)	7000[d]	0.19	Soil burrow	High–intermediate	1230/954	
		Striped desert hamster (*Phodopus sungorus*)	23.4	57.69	Soil burrow	High–intermediate	1230/7020	
		Jerboas (Dipodidae)	30[d]	45.0	Soil burrow	High–intermediate	NA	
		Zokor (*Myospalax* spp.)	225	6.0	Soil burrow	High–intermediate	NA	
European polecat (*Mustela putorius*)	1100	European rabbit (*Oryctolagus cuniculus*)	2150	0.51	Soil burrow	Intermediate	12,200/26,800	Bomberg (1937); Matthews (1952); Brugge (1977); Jaksic and Soriguer (1981); Clark (1983); Blandford (1987)
Pacific marten (*Martes caurina*)[b]	1250	Douglas squirrel (*Tamiasciurus douglasii*)	225	5.55	Middens (winter)	Intermediate	24,000/914	Simon (1980); Zielinski et al. (1983); Spencer (1987)
American marten (*Martes americana*)	1250	American red squirrel (*Tamiasciurus hudsonicus*)	201.2	6.21	Middens (winter)	Intermediate	24,000/5330	Raine (1981); Buskirk (1984)
European pine marten (*Martes martes*)	1300	Eurasian red squirrel (*Sciurus vulgaris*)	333	3.90	Dreys (nests)	Intermediate	100,000/10,700	Pulliainen and Ollinmäki (1996)
Sable (*Martes zibellina*)	1130	Eurasian red squirrel (*Sciurus vulgaris*)	333	3.39	Leaf nest	Intermediate	1360/10,700	Stroganov (1969)
Fisher (*Pekania pennanti*)[c]	4000	Eastern gray squirrel (*Sciurus carolinensis*)	506.5	7.90	Leaf nest	Intermediate	3410/9300	S. LaPoint (pers. comm.); R. Green (pers. comm.)
		Mountain beaver (*Aplodontia rufa*)	800[d]	5.0	Soil burrow	Intermediate	3410/1180	J. Lewis (pers. comm.)

Table 1 (continued)

Predator species	Predator weight (g)	Prey species	Prey weight (g)	Predator/ prey weight	Type of refuge	Latitude[a]	Number of Google Scholar references Predator/prey	References
		Amercian porcupine (*Erethizon dorsatum*)	7085.3	0.56	Cavity den in tree	Intermediate	3410/3060	R. Powell (pers. comm.)
Marbled polecat (*Vormela peregusna*)	543	Great gerbil (*Rhombomys opimus*)	175[d]	3.10	Soil burrow	High–intermediate	575/1980	Heptner and Naumov (1974); Roberts (1977); Gorsuch and Lariviére (2005).
		Libyan jird (*Meriones libycus*)	91.3	5.95	Soil burrow	Intermediate	575/1310	
Egyptian mongoose (*Herpestes ichneumon*)	2850	European rabbit (*Oryctolagus cuniculus*)	2150	1.32	Soil burrow	Low	1880/26,800	Palomares and Delibes (1993); Palomares et al. (1995)
Yellow mongoose (*Cynictus penicillata*)	836	Termite (Blattodea)			Termite mound	Intermediate	NA	Nel and Kok (1999)
Kit fox (*Vulpes macrotis*)	2100	Black-tailed prairie dog (*Cynomys ludovicianus*)	1364	1.40	Soil burrow	Intermediate	3090/5700	Morrell (1972); Cypher (2003); List and Macdonald (2003)
		Kangaroo rats (*Dipodomys* spp.)	85	24.70	Soil burrow	Intermediate	NA	
		California ground squirrel (*Otospermophilus beecheyi*)	578.5	3.63	Soil burrow	Intermediate	3090/2970	
Swift fox (*Vulpes velox*)	2197.5	Kangaroo rats (*Dipodomys* spp.)	85	25.85	Soil burrow	Intermediate	NA	Kilgore (1969); Uresk and Sharps (1986); Cypher (2003)
		Black-tailed prairie dog (*Cynomys* sp.)	1364	1.61	Soil burrow	Intermediate	NA	
Average				10.51				
SD				18.55				
Average (without mongoose—termite)				8.15				
SD (without mongoose—termite)				13.8				

Predator and prey weights, with a few exceptions, were acquired from an online database which averaged sexes and geographic locations for each species (Smith et al. 2003). Latitude represents the general distribution of the prey and predator, and "Number of Google Scholar References Predator/Prey" represents the number of results returned from a query of each species' scientific name on 14 October 2014. The number of references for the predator is the numerator and number for the prey species is the denominator

[a] Low = approximately between 20° N and 20° S; Intermediate = approximately between 20 and 40° N or S; High >60° N or S

[b] The Pacific marten (*Martes caurina*) was formerly the American marten (*Martes americana*) in western North America (Dawson and Cook 2012)

[c] The fisher (*Pekania pennanti*) was formerly *Martes pennanti* (see Sato et al. 2012)

[d] Body weight acquired via a web source other than Smith et al. (2003)

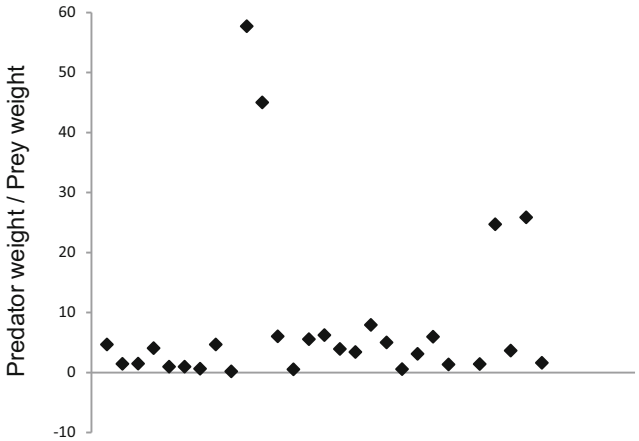

Fig. 1 Distribution of ratios of predator weight/prey weight for species for which the appropriation of refuges of key prey has been reported. The four outliers, with ratios >20, are (1) steppe polecat—striped desert hamster, (2) steppe polecat—jerboa, (3) kit fox—kangaroo rat, and (4) swift fox—kangaroo rat

during the winter when their prey require reinforced and thermally secure refugia, which the predators—provided they are small enough—can also benefit from appropriating.

The four species pairs that have body weight ratios that far exceed 10 are interesting to consider further. Two of the pairs involved the steppe polecat and two species of relatively small mammals that dig burrows in soil. The polecat is a long and thin predator which, despite its weight, can probably exploit the relatively small diameter burrows of the gerbil and jerboa. The other two pairs involve the congeneric kit and swift foxes and their kangaroo rat prey. The foxes are small canids but their use of the kangaroo rat burrows is probably possible because the rats enlarge their burrows beyond the minimum size necessary to accommodate their own bodies (Vorhies and Taylor 1922).

Why doesn't the behavior of co-opting the refugia of prey occur more often in other families within the Carnivora? Large carnivores (e.g., large cats, wolves, bears) typically prey on large prey that do not build refuges, nor do the larger carnivores always use refuges because they have fewer predators themselves or live in moderate climates. This excluded most of the larger species in the Canidae, Ursidae, Felidae, and Hyaenidae. And, the phenomenon of usurping prey refugia does not typically apply to insectivores or frugivores, which excluded many of the Mephitidae, Herpestidae, Viverridae, and Ursidae. Most of the canids are significantly larger than their prey (often exceeding the ratio of predator–prey size described here), and thereby have limited options for exploiting the shelters of their prey. The exceptions are the small foxes that regularly use burrows for shelter, including, for example, the swift fox (*Vulpes velox*), kit fox (*Vulpes macrotis*), and corsac fox (*V. corsac*). The latter uses the burrows of the Siberian marmot (*M. sibirica*) but does not prey on this relatively large herbivore (Murdoch et al. 2010). However, the swift and kit foxes are small carnivores (1–3 kg) that use a complex array of burrows and dens and, unlike other canids, use subterranean burrows daily, not just as natal dens (Cypher 2003). Individual kit foxes, for example, may use dozens of den sites in a year (Reese et al. 1992). Swift and kit foxes enlarge or appropriate refuges from species of granivores and herbivores that are significant components of their diet, particularly kangaroo rats (*Dipodomys* spp.) and prairie dogs (*Cynomys* spp.), making them among few species of canids that can kill, and then exploit for their own use the refugia of their prey.

I found no evidence of felids involved in this behavior, probably because they rarely hunt in enclosed spaces, exploiting a stalking strategy that requires detecting prey movement. Moreover, many small cats hunt birds and lagomorphs (Sunquiest and Sunquist 2009), neither of which typically create refugia that may be useful to their predators. It is, perhaps, more surprising that there are not more accounts of the appropriation of prey refugia reported for viverrids or herpestids, many of which use burrows or other holes in the ground or in trees (Gilchrist et al. 2009; Jennings and Veron 2009) and are small enough to enter the spaces occupied by small herbivores (particularly the more slender and smaller species that use open terrain habitats where they occupy soil burrows). However, many are frugivorous and insectivorous (there are only seven species in the Herpestidae that are reported as feeding on vertebrates [Gilchrist et al. 2009]). It may be that because viverrids and herpestids are primarily old world and tropical or subtropical, less is known about their feeding and resting ecology than for many mammals in North America or Europe. The absence of reports of the behavior in these two families suggests the need for research on their predatory behavior and, in general, to determine the occurrence of the appropriation of prey refugia by small and mid-sized carnivores in the tropics and subtropics.

It is important to distinguish the species that exploit prey for both food and refuge as a regular strategy versus those that do it only occasionally. The former would appear to have a stronger dependence on their prey, one that could put the predator at risk if the prey's populations decline due to human disturbances/exploitation or to changes in the prey's habitat, or spatio-temporal availability as a result of climate change, for example. Indeed, predators that depend on the use of their prey's refugia, and whose fates are linked strongly to a few key prey species for this reason (particularly the *Mustela* of the northern latitudes) may be particularly vulnerable to changes in climate that affect the subnivean habitat of their prey (Pauli et al. 2013) since it is within the subnivean zone that winter nests are created. More broadly, mammals that create refugia that can be used by other species (among them predators) may play an important—if not keystone (Power et al. 1996)—role in the communities in which they occur (Zhang et al. 2003; Murdoch et al. 2013). This provides

additional incentive for the research community to investigate further the importance of prey that provides both food and shelter for predators.

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